



# Contrasting river migrations of Common Snook between two Florida rivers using acoustic telemetry

R.E. Boucek<sup>a,\*</sup>, A.A. Trotter<sup>b</sup>, D.A. Blewett<sup>c</sup>, J.L. Ritch<sup>b</sup>, R. Santos<sup>d</sup>, P.W. Stevens<sup>b</sup>, J.A. Massie<sup>d</sup>, J. Rehage<sup>d</sup>

<sup>a</sup> Bonefish and Tarpon Trust, Florida Keys Initiative Marathon Florida, 33050, United States

<sup>b</sup> Florida Fish and Wildlife Conservation Commission, Florida Fish and Wildlife Research Institute, 100 8<sup>th</sup> Ave. Southeast, St Petersburg, FL, 33701, United States

<sup>c</sup> Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Charlotte Harbor Field Laboratory, 585 Prineville Street, Port Charlotte, FL, 33954, United States

<sup>d</sup> Earth and Environmental Sciences, Florida International University, 11200 SW 8<sup>th</sup> street, AHC5 389, Miami, Florida, 33199, United States

## ARTICLE INFO

Handled by George A. Rose

### Keywords:

Spawning migration  
Common snook  
Everglades national park  
Caloosahatchee river  
Acoustic telemetry,

## ABSTRACT

The widespread use of electronic tags allows us to ask new questions regarding how and why animal movements vary across ecosystems. Common Snook (*Centropomus undecimalis*) is a tropical estuarine sportfish that have been well studied throughout the state of Florida, including multiple acoustic telemetry studies. Here, we ask; do the spawning behaviors of Common Snook vary across two Florida coastal rivers that differ considerably along a gradient of anthropogenic change? We tracked Common Snook migrations toward and away from spawning sites using acoustic telemetry in the Shark River (U.S.), and compared those migrations with results from a previously published Common Snook tracking study in the Caloosahatchee River. We found that the proportions of fish that did not migrate out of rivers during the spawning season and presumably skip spawned were similar between the two systems. However, in the Shark River, there was more year-to-year variability in this behavior, likely tied to freshwater flow and floodplain inundation. Second, we found that the length of time individuals spent outside of rivers during the spawning season (i.e. proxy for time spent spawning) was less in the Shark River than in the Caloosahatchee. Last, the proportion of Snook at emigrated and did not return in the Shark River was higher than in the Caloosahatchee. These latter finding could reflect higher straying rates or higher mortality at spawning grounds. Future work should evaluate whether these spatial differences in river migrations are meaningful enough to affect management. This study illustrates that cross-site comparisons can improve confidence in our understanding of life history metrics while also highlighting differences between sites that are worth exploring to gain a better understanding of a species plasticity in adapting to their environment.

## 1. Introduction

The development, affordability, and now widespread use of electronic tags and other animal tracking technologies has provided new opportunities for research that improves fisheries management and conservation (Crossin et al., 2017). One such opportunity is comparing how, in what ways, and why animal behavior varies across ecosystems. These cross-site comparative studies have important applications for fisheries management and conservation. We can use changes in animal behaviors to evaluate restoration success by conducting telemetry studies in one system treated with a management intervention, relative to another control habitat or ecosystem (Reynolds et al., 2010; Eggenberger et al., 2018). Likewise, paralleling telemetry studies control for,

and isolate, a few environmental variables to help us measure processes relevant for assessment, such as the interaction of temperature and depth on the effects of barotrauma (Jackson et al., 2018). Here we present a case-study featured in the special issue ‘Using telemetry for cross-ecosystem comparisons of animal behaviors’. Our study demonstrates the utility, and obstacles to be overcome, of cross-site comparative research by contrasting spawning migrations of a euryhaline sportfish, across two distinct coastal rivers.

Common Snook, (*Centropomus undecimalis*; referred to as Snook throughout) are a tropical estuarine sportfish, prized for both their table-fare and fighting abilities (Muller et al., 2015). Snook are highly fecund, marine obligate batch spawning species that form spawning aggregations at barrier islands, river mouths, and on offshore wrecks

\* Corresponding author.

E-mail address: [Ross@bonefishtarpontrust.org](mailto:Ross@bonefishtarpontrust.org) (R.E. Boucek).

<https://doi.org/10.1016/j.fishres.2018.12.017>

Received 28 April 2018; Received in revised form 14 December 2018; Accepted 17 December 2018

Available online 06 February 2019

0165-7836/ © 2018 Published by Elsevier B.V.

and reefs during the spring and summer months (Taylor et al., 1998). Snook in Florida are currently managed as two stocks, an Atlantic and a Gulf of Mexico stock (Muller et al., 2015). This two-stock designation is based off genetic differences between Snook found between those ocean basins. Previous acoustic telemetry research on the Gulf of Mexico and in the Atlantic Ocean show that Snook exhibit high spawning site fidelity (Adams et al., 2011; Lowerre-Barbieri et al., 2014; Young et al., 2014, 2016). Likewise in the Gulf of Mexico, external tagging projects, and extensive telemetry studies (> 120 fish tagged over six years) show Snook generally do not move between estuaries (Trotter unpub. data; Muller et al., 2015; Boucek et al., 2017b). These lines of evidence and others (Stevens et al., 2016, 2018), potentially provide a scenario where management at finer spatial scales (unit of an estuary) could improve sustainability. Cross-site comparative research using telemetry provides an opportunity to test whether snook spawning behaviors relevant to assessment may also vary across estuaries, giving another line of evidence for evaluating more spatially explicit management (Adams et al., 2009; Trotter et al., 2012; Lowerre-Barbieri et al., 2014; Young et al., 2014; Boucek et al., 2017a).

We compared spawning migrations in two Florida coastal rivers, Caloosahatchee and Shark River. These river systems feed two estuaries that are separated by over 200 km. Importantly, these systems sit on opposite sides of a gradient of anthropogenic change. The Caloosahatchee River, which is best described as a cross-state canal (Bass and Cox, 1985), lies on the more degraded end. The surrounding watershed for this river is developed for residential and agricultural uses, water quality due to nutrient enrichment from upstream water sources can be poor, and the river system is mesotrophic. Last, the hydrologic regime differs from the natural regime, with the river now receiving sporadic high volume pulses of nutrient rich freshwater driven from flood control measures upstream (Doering et al., 2002). In contrast, the Shark River occurs in the center of a World Heritage Site, the river morphology is completely natural, shorelines are mangrove fringed, and though the current volume of freshwater the river received historically is less, the seasonality of freshwater inputs remains largely the same (Childers, 2006; Boucek and Rehage, 2013, 2015). These two river systems provide interesting contrasts, because they likely differ on many processes that could influence spawning behaviors and therefore the productivity of those populations (Table 1).

Trotter et al. (2012) described the spawning behaviors of Snook within the Caloosahatchee River with acoustic telemetry from 2005–2007. Here, we compare spawning behaviors of Snook measured in Trotter et al. (2012) with an ongoing tracking study within the Shark River. We compare three migration behaviors that may reflect trends in spawning effort, 1) the number of fish that did not migrate and presumably skip spawned, 2) the # of days snook spent outside of rivers during the spawning season, and 3) the proportion of snook that didn't return to rivers following spawning. We acknowledge that in comparing habitat use of a species in these two systems, there will be methodical

challenges to consider. For example, it is difficult to perfectly replicate telemetry array design, detection efficiency, study duration, and tagged fish demographics. We discuss these potential limitations and how they may have influenced our results in the discussion.

## 2. Methods

### 2.1. Study system: Caloosahatchee River

The Caloosahatchee River is one of three rivers that supply freshwater to Charlotte Harbor, an estuary located along the southwest coast of Florida (Fig. 1; Table 1). The river has been altered to create the cross-Florida Okeechobee Waterway that connects Lake Okeechobee at its western terminus to the southern Charlotte Harbor estuarine system. Three locks regulate the river flows and lake levels and facilitate navigation from the lake to the Gulf of Mexico. The river courses approximately 121 river kilometers (1 rkm = 1000 m along the mid-line of the main stem of the river), drains 3569 km<sup>2</sup>, and discharges an average of 40.8 m<sup>3</sup>s<sup>-1</sup> annually (Hammett, 1990). The study took place at the lower portion of the river, below the S-79 lock. Along this section of the river, 57% of the watershed is developed (42% agriculture; 15% residential), and is mesotrophic throughout ( $\approx 15 \mu\text{g/L}$ ; SFWMD 2005). Salinity regimes below the S-79 lock are generally fresh to about river kilometer 35. The watershed on average receives 132 cm/yr in rainfall, though freshwater flows and salinities are largely influenced by freshwater release schedules occurring upstream. River characteristics are summarized in Table 1. Salinity fluctuations in the system are seasonal, with up to 10 PSU values recorded at the upstream Franklin lock in the dry season. In contrast, during the wet season, salinities often reach 5 PSU at the mouth of the river.

### 2.2. Study system: Shark River everglades

The Shark River system and surrounding watershed, located within Everglades National Park in South Florida (U.S.), is federally protected by the National Park Service (Fig. 1). Unlike the Caloosahatchee, the river is braided, and relatively shorter (approximately 31 river KM). Despite being a relatively short river, this system is the terminus for the Shark River Slough, the largest freshwater drainage of the southern Everglades. The Shark river experiences a pronounced hydrologic seasonality, that matches seasonal rainfall with 80% of annual rainfall occurring in the summer and fall (July–November; Price et al., 2008). Except during droughts, the upstream 10 KM of the river is generally below 5 PSU year-round. From River KM 15 to river KM 25, salinities vary from below 5 PSU to 15–25 PSU, and below that, the river is largely tidal, ranging from 15 PSU to marine water. Shark river productivity increases on a gradient from upstream to downstream. In this estuary, oligotrophic freshwater inputs create an upstream-downstream gradient of productivity, with phosphorus limited conditions upstream and more productive conditions downstream, fueled by marine derived phosphorous subsidies (Childers, 2006; Ewe et al., 2006). River characteristics are summarized in Table 1.

### 2.3. Tagging and tracking spawning behaviors

Since Snook are both euryhaline, and marine obligate spawners (> 24 PSU for successful spawning), those fish occupying freshwater systems are assumed to not spawn (Ager et al., 1978). Thus, tracking Snook migration patterns out of the freshwater environment (< 6 PSU) to the terminus of the river systems and to marine environment (> 24 PSU) during the spawning season can provide a measure of spawning activity and behaviors (Trotter et al., 2012). During the spawning season, in the Caloosahatchee River, salinities at the mouth of the river are too low for successful spawning except during drought (Trotter et al., 2012). In the Shark River, salinities early in the spawning season create conditions where snook could spawn in the river mouths.

**Table 1**

Characteristics of the two river systems used in this cross-site comparisons. All information is available through South Florida Water Management District, and Southwest Florida Water Management Districts.

	Caloosahatchee	Shark River
River length river KM	121	31
Watershed KM <sup>2</sup>	3569	1,700
Discharge (m <sup>3</sup> s <sup>-1</sup> )	40.8	9.3
Watershed development	57%	0%
River morphology	straight	braided
Flow regime	highly regulated	natural
Rainfall in basin cm/yr	132	128
Human populations in watershed	822,800	0
Chlorophyll $\alpha$ ( $\mu\text{g/L}$ )	12	1.4
Ave water temperature °C <sup>a</sup>	26.4	25.9

<sup>a</sup> means across upper, middle, and lower coastal.

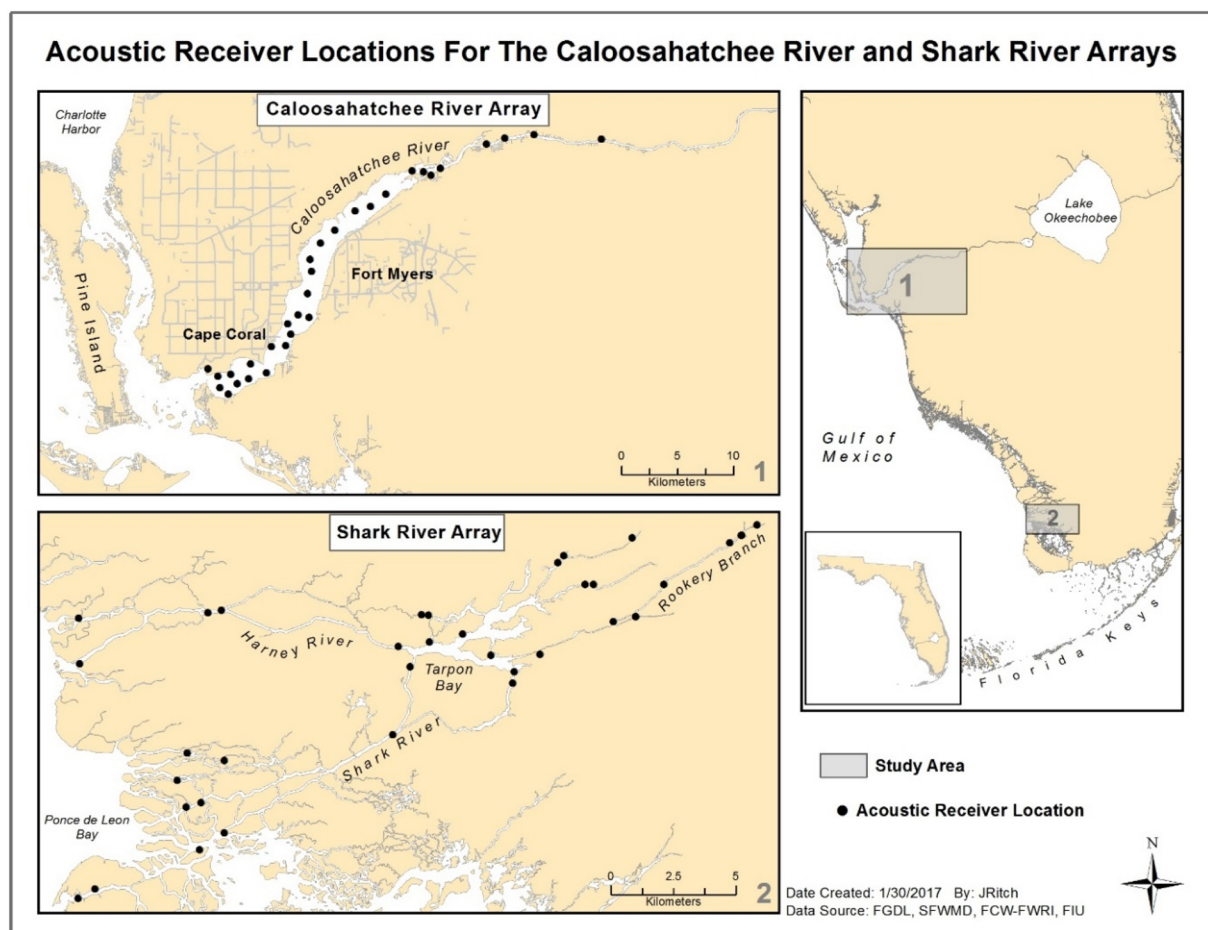


Fig. 1. Map of both study locations. Black dots represent acoustic receivers.

However, repeated sampling efforts via hook and line during the evenings of new and full moons did not produce any snook with hydrated oocytes or post ovulatory follicles in river mouths of Everglades National Park, suggesting spawning occurs elsewhere (Boucek et al. unpublished data).

We tracked the movements of individual Snook using acoustic telemetry. In the Caloosahatchee River, Trotter et al. (2012) used a network of 31 acoustic (VECMO VR2) receivers which were evenly spaced throughout the river system (Fig. 1; see Trotter et al., 2012 for more details). To track migrations of Snook in the Shark River, we used a similar array configuration in (37 VR2W receivers, Fig. 1; Rosenblatt and Heithaus, 2011; Boucek et al., 2017b). In the Caloosahatchee, detection ranges across the river were 500 M. In the Shark River, upstream receivers (upstream of 15 river KM), detection ranges were 500 M. Below 15 river KM, detection ranges decrease to 50–75 M. Receivers in the array were spaced approximately 1 KM apart, extending from the upper reaches of the Shark River down to the coastal regions of the Shark and Harney River systems. In this river, the southwest portion becomes more braided, and receiver coverage is not as complete as it is in the upstream portions. The receiver's locations that are in place in the braided region were selected because those areas represent the major flow paths for freshwater discharge.

Snook were captured in both systems using boat-mounted, generator-powered electrofishers in the freshwater portions of the rivers (see Trotter et al., 2012; Boucek and Rehage, 2013; for a more detailed description). Upon capture and prior to tagging, Snook were measured, weighed (only in the Shark River), and internally marked with a Passive Integrated Transponder (PIT) tag in the Shark River or an external dart tag in the Caloosahatchee River to identify recaptures. Prior to tagging

surgeries, Snook were placed in a container and were anesthetized in an ambient water and Alka-Seltzer solution (1 to 1.5 tablets per four liters of water; Adams et al., 2009). Once a fish was anesthetized, fish were moved to another holding container with ambient water and were placed in an angled cradle, such that water submerged their gills while leaving the abdomen above water. In the Caloosahatchee, water was pumped over the gills on Snook while they lay on a wetted flat surface (Trotter et al., 2012). At this time, a 30 mm incision was cut in the lower abdomen and each individual was surgically fitted with either a VEMCO V16 or V13 transmitter (interpulse delay, 120 s) and wounds were closed with one to four stitches (Trotter et al., 2012; Boucek et al., 2017b). V16 tags are larger in diameter, have longer battery life, and can be detected from further away than V13 tags. In the Caloosahatchee, 25 Snook were tagged in May of 2005, with a mean total length (TL) of 76.1 (SE  $\pm$  3.2 cm). In the Shark River, a total of 96 fish were tagged, 41 transmitters were deployed in 2012, 16 tags in 2013, 19 tags in 2014, and 20 tags in 2015. In the Shark River, 70% of fish were tagged in the spring months and 30% were tagged in the fall. The average TL for Snook tagged in the Shark River was 71.9 cm (SE  $\pm$  .83 cm), and that length did not differ (students t-test,  $p = .069$ ) from fish tagged in the Caloosahatchee. In both studies, sexes of individuals were not recorded. We can infer the probability of a Snook being a male or female based off body length (Muller et al., 2015). Based off the lengths of the tagged population, the probability at the time of tagging that a Snook was a female in both systems is 0.64 and 0.85.

We quantified three different spawning behaviors of Everglades Snook using the same methods as Trotter et al. (2012). We calculated 1) proportion of fish that never left rivers during the spawning season (index of skip spawning), 2) time spent outside rivers, defined as the

time between when a fish moved out of the freshwaters, was last detected on receiver at rivermouths, and then detected again within the array (i.e. a proxy for the duration of spawning). And, 3) the proportion of fish that left the rivers but never returned (index of facultative catadromy and possibly spawning survival; Lowerre-Barbieri et al., 2014) by tracking the movements of Snook in and out of non-spawning habitats during the months of April through September. For those fish that never returned back to rivers, Trotter et al. (2012) were able to distinguish fish that were harvested outside rivers (anglers report harvesting a dart tagged fish), however, in the Shark River, where we used internal PIT tags, we were not. Thus, for comparisons, we considered fish in the Caloosahatchee River that migrated outside of the river and were harvested as a fish that left the river and did not return. For statistical comparisons, we needed to use multiple tests. For fish that never left the river during a spawning season, we calculated the mean and 95% confidence intervals of the yearly average proportion of Snook that migrated out of the Caloosahatchee River and the Shark River. Likewise, for the duration of time individuals spent downstream of the arrays, we calculated the mean and 95% confidence intervals for the number of days individuals spent outside of rivers for both systems. Confidence intervals were built from a bootstrapped distribution that resampled yearly mean proportions or number of days spent outside rivers with 1000 simulations. If these confidence intervals did not overlap, we determined there were differences in those behaviors between the two rivers. Due to sample size limitations in the Caloosahatchee, for proportion of fish that migrated out of rivers and did not return, we compared the total proportion of fish that permanently emigrated from Trotter et al. (2012), to the proportion of permanent migrants each year in the Shark River with Chi squared tests.

### 3. Results

Over the course of the Shark River study, the average number of days we detected a Snook on a receiver was 344 days ( $\pm$  33 days SE, range = 15–912 days). We did not detect 14 of the 96 fish we tagged, indicating post release survival of around 85%. On average, we tracked 26 Snook per day ( $\pm$  1 snook SE, range = 18–35). Across the four years of study in the Shark River, we observed 71 out-river migrations, where fish moved downstream and were last detected on the most western receivers. For detailed descriptions of the Caloosahatchee River tracking information, see Trotter et al. (2012).

When we compare how many Snook left rivers during the spawning season, we found that the three-year average in the Caloosahatchee River and the four-year average in the Shark River were not different, (0.62 in the Caloosahatchee River vs. 0.55 in the Shark River of tracked fish left rivers per year; Fig. 2b). However, the year to year variability seems to be higher in the Shark River. In 2012 and 2015 the proportion of fish that left the river (.78 & .72) exceeded the 95% confidence intervals around the three-year average of the Caloosahatchee River study. In 2013 and 2014, the proportion of fish that left the river during

the spawning season in the Shark River fell below 95% confidence intervals around the three-year average in the Caloosahatchee River (.20 and .51).

Moving to the time Snook spent outside of rivers during the spawning season. Individual Shark River Snook spent an average of 42 days outside of the river, falling below the 95% confidence intervals that surround the three year average duration Caloosahatchee River fish spent outside of rivers (mean 77 days; Fig. 3). In the Shark River, this behavior was relatively consistent across years, except for 2013, when only one fish that left the river system returned. That fish was absent from the Shark River for five days.

Last, the proportion of Snook that returned to the Shark River varied somewhat across years (0.16–0.47 proportion of return migrants). For three of the four years of study, the proportion of Snook that returned to rivers following the spawning season was less than the proportion of fish that migrated and returned back Caloosahatchee River (60% of emigrants returned;  $\chi^2 > 4.8$ ,  $p < 0.05$ ). 2014 was the exception, and was not different than the Caloosahatchee River, where 47% of fish that left the river returned at the end of the spawning season (Fig. 4).

### 4. Discussion

Telemetry research networks provide a platform to facilitate cross-ecosystem studies of animal movements examined here (Boucek and Morelly, 2018). Due to the increasing affordability of this technology and its capacity to study animal behavior at both broad and fine-scale spatial-temporal resolutions, passive acoustic-telemetry infrastructure is in place in nearly every coastal and nearshore ecosystem in the United States and in other nations (Hussey et al., 2015). The now widespread use of this infrastructure has led to the emergence of telemetry networks that connect researchers using telemetry at the regional (e.g. integrated Tracking of Aquatic Animals Across the Gulf of Mexico iTAG) and even the global level (Ocean Tracking Network, OTN; Boucek and Morelly, 2018; Hussey et al., 2015). This study, and many in this special issue, were a product of telemetry researchers meeting and collaborating through the iTAG network. Meeting and communicating regularly through these networks builds trust among the telemetry research community allowing for more open communication and datasharing (Nguyen et al., 2017; Boucek and Morelly, 2018). As telemetry networks continue to emerge and grow, including and building cross ecosystem comparative studies into their mission will likely improve the science done by these networks.

In this study, cross-site comparisons revealed both consistencies and differences in Snook spawning behaviors between the two ecosystems currently managed as a single stock, which may merit more directed follow up studies. First, we found that the proportions of fish that did not migrate out of rivers during the spawning season and presumably skip spawned were similar between the two systems. However, in the Shark River, there was more year-to-year variability in this behavior. Second, we found that the length of time individuals spent outside of

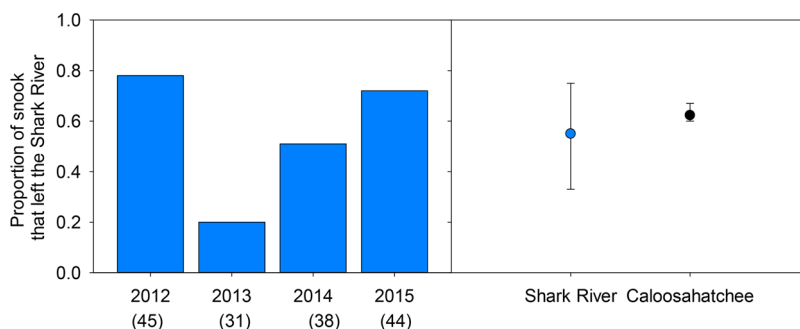
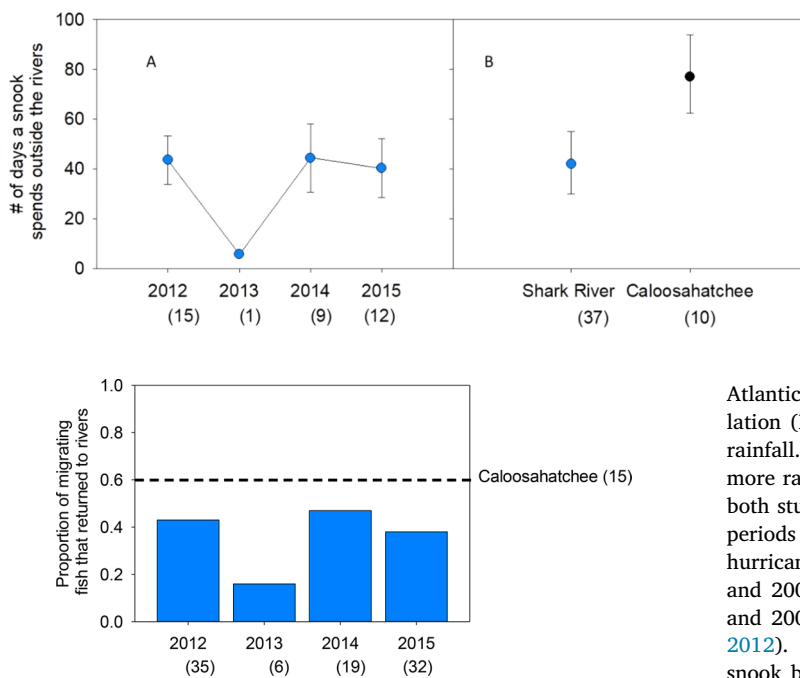


Fig. 2. A) The proportion of fish that migrated out of the Shark river per year. Numbers below panel (A) show the number of Snook tracked during that year's spawning season. B) The annual average proportion and 95% C.I.s of Snook that migrated out of both rivers.





**Fig. 3.** A) The average number of days that an individual Snook spent outside of the Shark River per year. Error bars show  $1 \pm$  SE. The numbers below panel (A) show the number of complete migrations from Shark River per year. B) The mean and 95% C.I. of the average number of days an individual Snook spent outside of rivers in both systems. Numbers below the figures represent the total number of complete migrations.

**Fig. 4.** Proportion of complete river migrations in the Shark River each year. Black dashed line represents the Proportion of complete river migrations from Caloosahatchee River, from Trotter et al. (2012). Numbers in parentheses are the total number of emigrations in the Shark River per year. Number next to the dotted line shows the total of number emigrations in the Caloosahatchee River.

rivers during the spawning season was less in the Shark River than in the Caloosahatchee River. Last, the number of permanent emigrants in the Shark River was higher than in the Caloosahatchee River. Future work should explore mechanisms explaining these differences, including the possibility of methodical factors such as array design, and evaluate whether these spatial differences in river migrations are meaningful enough to affect the population dynamics of snook and their resilience to fishing and other environmental drivers.

Inherent differences in the geomorphology of the two coastal rivers could have influenced our results, with the Caloosahatchee River being a wider, longer river, and the Shark river that is shorter, narrower, and braided. Under the array configuration in the Shark River, there are areas where fish could enter a part of the system and remain undetected. This array configuration could influence two metrics we use for comparisons; the duration individuals spend outside of rivers and proportion of permanent emigrants. There is a possibility that snook in the Shark river are spending less time outside of rivers and are not detected until they move further into the core array. We think this scenario is unlikely. In the Shark river, Snook spend approximately 40 days outside of the system, which is approximately the same number of days snook spend at spawning sites seen in other studies (Boucek et al., 2017a; Young et al., 2014; Lowerre-Barbieri et al., 2014). When considering the proportion of fish that were marked as permanent emigrants, Snook could have spawned and returned to the Shark River, but took up residence in the braided channels, where coverage is limited. Under this scenario, it would appear as though the fish had migrated and never returned to the system. In the Shark river, Snook are somewhat mobile, moving up to 3 KM per day. Even if fish did take up residence in a different section of the river, they would eventually pass a receiver in that area, marking its return.

A second limitation in our cross-site comparison is the temporal mismatch of the two studies. Trotter et al. (2012) occurred from 2005 to 2007, whereas the Shark river tracking study occurred from 2012 to 2015. In South Florida, year to year variability rainfall and temperature are driven by large-scale ocean atmospheric teleconnections including

Atlantic Multi-decadal Oscillation (AMO) and El Nino Southern Oscillation (ENSO). In the positive phase of AMO, summers receive more rainfall. In the positive phase of ENSO, winters are warmer and receive more rainfall (Moses et al., 2013). AMO was in the positive phase for both studies, and ENSO showed similar variability between both time periods (<http://www.cpc.ncep.noaa.gov/>). At finer spatial scales, two hurricanes passed over the Caloosahatchee River watershed in the 2004 and 2005, causing higher than normal freshwater discharge in 2005 and 2006. In 2007 the system experienced a drought (Trotter et al., 2012). Nevertheless, there were remarkable consistencies between snook behavior in the Caloosahatchee and Shark Rivers during these disparate time series in a general sense, while some key differences have been identified that can now be explored further.

In the Shark River, interannual variation in freshwater flow may influence the spawning behaviors of snook. We observed relatively high levels of interannual variability in the number of fish that didn't migrate out of the Shark River during the spawning season that could be linked to freshwater flows. An important driver of skip spawning is energetics. For instance, in Norway, the likelihood that Atlantic Cod (*Gadus morhua*) will spawn forms a non-linear relationship with fish condition (Skjæraasen et al., 2012). The probability of an individual skip spawning is high for fish at very low condition states, as individuals do not have the necessary energetic reserves to allocate to migration and reproduction. At the opposite end of the spectrum, the probability of skip spawning increases for fish in very high condition states. For Cod in abnormally high condition, investing extra energy reserves into growth instead of reproduction is expected to increase lifetime fecundity, with reproduction in future years at a larger size exceeding a single year of high reproductive output at a smaller size (Jørgensen et al., 2008; Skjæraasen et al., 2012). In the freshwater region of the Shark River, prey availability can vary by an order of magnitude from year to year based on hydrologic conditions that inundate floodplains crowning the system (Boucek et al., 2016). Similar linkages between freshwater flow and prey abundance have been documented in other Florida Rivers with intact watersheds (Blewett et al., 2017). In 2013, a year when river fidelity or skip spawning in the Shark river was approximately 80%, prey biomass in the Shark River was the highest recorded during the 12 year time series (Boucek and Rehage, 2014; Boucek et al., 2016), and consequently Snook condition was higher than the other years of this study (Rehage unpub. Data). During that year, Snook may have invested those energy reserves in growth or other ontogenetic processes that would increase lifetime fecundity and forewent spawning. Interannual differences in skip spawning were not apparent in the Caloosahatchee River study.

The number of days that individual Snook spent outside of rivers varied across systems. In other telemetry studies on the East coast of Florida and in Tampa Bay (FL), Snook generally spend 40 days at spawning aggregation sites, matching the findings from the Shark River (Lowerre-Barbieri et al., 2014; Young et al., 2014; Boucek et al., 2017a). Unlike these other systems, Caloosahatchee River Snook spent approximately 70 days outside of rivers. One possibility is that since we did not identify the sex of tagged fish, that the Caloosahatchee River

may have by chance tagged a higher proportion of females. Previous work on Snook has shown that females will spend more time at spawning sites than males (Young et al., 2014). If, in fact Caloosahatchee River fish are spending longer times at aggregation sites, may create a point of vulnerability for the fishery. For instance, Muller et al. (2015), note that the majority of harvest for Snook occurs at aggregation sites before and after the closed harvest season for Snook. Thus, if Snook are spending longer times at these aggregation sites, Caloosahatchee River Snook vulnerability to harvest may be higher than in the Shark River. The ecological underpinnings of how these differences in the duration individuals spend outside of the rivers during the spawning season, and how that may translate to vulnerability to fishing and disturbance, should be explored further.

Last, the proportion of fish that showed fidelity to rivers following the spawning season was surprisingly low in both studies, though lower in the Shark River. Two plausible explanations exist that could explain this low fidelity to rivers. First, the degree of straying for Snook may be relatively high. Another consideration is that mortality outside rivers at spawning sites could result in a signal of incomplete migration. At the aggregation sites outside of the Shark River during the spawning season, high rates of angling related shark predation is a concern that anglers have voiced, especially for larger size classes of Snook (Boucek personal observation). Similar to the Shark River, in the Caloosahatchee River and in nearby spawning aggregation sites, anglers are reporting that depredation and post-release predation by cetaceans (A. Trotter, personal communication). For Snook, as well as for other aggregating species, anglers concentrate effort on aggregations because catch rates are high (Young et al., 2014; Erisman et al., 2017). Even if the fishery is entirely catch and release, in high predator environments, depredation and post-release mortality can be as high as 60–90% (Danylchuk et al., 2011; Adams and Murchie, 2015). In Florida and throughout the Southeast United States, because of effective conservation actions, shark populations are at the highest they have been in 20 years (Peterson et al., 2017). The effect of fishing induced predation from sharks and cetaceans on the sustainability of fish like snook that are a virtually catch and release is a critical research priority, and we must be proactive in developing management frameworks that mitigate impact.

This cross-site comparison illustrates how findings from more than one location can provide more confidence in biological metrics and the conceptual life history models that are developed from them, while also highlighting some of the challenges associated with a cross-site approach. For instance, ecological systems are rarely able to serve as perfect replicates, or ideally set up for control versus manipulation studies. Likewise, array configurations and detection efficiency can differ, limiting effective comparisons. And third, cross-site comparisons and synthesis are often a secondary consideration or value-added component of single ecosystem study. In those cases, differences in time scales of study, sample sizes, tagged animal demographics, etc. may create challenges for cross-site synthesis. To overcome these challenges in other fields of ecology, Peters et al., (2011) built a conceptual framework for developing more quantitative cross-site comparisons to better understand ecological responses to disturbance. Similarly, others have used interventional analyses instead of experiments with controls and replicates to potentially overcome some of the challenges with cross-site comparative studies (Underwood, 1994; Trexler et al., 2005). As natural sciences and animal tracking continues to move from isolated research that focuses single ecosystems, to more collaborative studies that understand processes at the regional or even global scale, models that facilitate these cross-site studies will only improve.

## Acknowledgements

This project is funded by the Monitoring and Assessment Plan of the Comprehensive Everglades Restoration Plan (CERP) through the US Army Corps of Engineers. This project was developed with support from the National Science Foundation (NSF) Water, Sustainability, and

Climate (WSC) program NSF EAR-1204762, and the Florida Coastal Everglades (FCE) Long Term Ecological Research (LTER) program (NSF DEB-1237517). This is contribution no. 114 from the Southeast Environmental Research Center at Florida International University.

## References

- Adams, A., Murchie, K., 2015. Recreational fisheries as conservation tools for mangrove habitats. *Am. Fish. Soc. Symp.* 83, 43–56.
- Adams, A., Wolfe, R.K., Barkowski, N., Overcash, D., 2009. Fidelity to spawning grounds by a catadromous fish, *centropomus undecimalis*. *Mar. Ecol. Prog. Ser.* 389, 213–222.
- Adams, A.J., Hill, J.E., Samoray, C., 2011. Characteristics of spawning ground fidelity by a diadromous fish: a multi-year perspective. *Environ. Biol. Fish.* 92, 403–411.
- Ager, L.A., Hammond, D.E., Ware, F., 1978. Artificial spawning of snook. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* 30 (1976), 158–166.
- Bass, D.G., Cox, D.T., 1985. River habitat and fishery resources of Florida. In: SEAMAN JR.W. (Ed.), *Florida Aquatic Habitat and Fishery Resources*. Florida Chapter of American Fisheries Society, Eustis, pp. 121–187.
- Blewett, D.A., Stevens, P.W., Carter, J., 2017. Ecological effects of river flooding on abundance and body condition of a large, euryhaline fish. *Mar. Ecol. Prog. Ser.* 563, 211–218.
- Boucek, R.E., Rehage, J.S., 2013. No free lunch: displaced marsh consumers regulate a prey subsidy to an estuarine consumer. *Oikos* 122, 1453–1464.
- Boucek, R.E., Rehage, J.S., 2014. Climate extremes drive changes in functional community structure. *Glob. Change Biol.* 20, 1821–1831.
- Boucek, R.E., Rehage, J.S., 2015. A tale of two fishes: using recreational angler records to examine the link between fish catches and floodplain connections in a subtropical coastal river. *Estuaries Coasts* 38, 124–135.
- Boucek, R.E., Soula, M., Tamayo, F., Rehage, J.S., 2016. A once in 10 year drought alters the magnitude and quality of a floodplain prey subsidy to coastal river fishes. *Can. J. Fish. Aquat. Sci.* 73, 1672–1678.
- Boucek, R., Leone, E., Walters-Burnsed, S., Bickford, J., Lowerre-Barbieri, S., 2017a. More than just a spawning location: examining fine scale space use of two estuarine fish species at a spawning aggregation site. *Front. Mar. Sci.* 4, 355.
- Boucek, R.E., Heithaus, M.R., Santos, R., Stevens, P., Rehage, J.S., 2017b. Can animal habitat use patterns influence their vulnerability to extreme climate events? An estuarine sportfish case study. *Glob. Change Biol.*
- Boucek, R. E., and Morelly, D. this issue. How do we get more cross-ecosystem comparative studies in acoustic telemetry research? *Fisheries Research*.
- Crossin, G.T., Heupel, M.R., Holbrook, C.M., Hussey, N.E., Lowerre-Barbieri, S.K., Nguyen, V.M., Raby, G.D., et al., 2017. Acoustic telemetry and fisheries management. *Ecol. Appl.* 27, 1031–1049.
- Danylchuk, A.J., Cooke, S.J., Goldberg, T.L., Suski, C.D., Murchie, K.J., Danylchuk, S.E., Shultz, A.D., et al., 2011. Aggregations and offshore movements as indicators of spawning activity of bonefish (*albulus vulpes*) in The Bahamas. *Mar. Biol.* 158, 1981–1999.
- Doering, P.H., Chamberlain, R.H., Haunert, D.E., 2002. Using submerged aquatic vegetation to establish minimum and maximum freshwater inflows to the caloosahatchee estuary, Florida. *Estuaries* 25, 1343–1354.
- Erisman, B., Heyman, W., Kobara, S., Ezer, T., Pittman, S., Aburto-Oropeza, O., Nemeth, R.S., 2017. Fish spawning aggregations: where well-placed management actions can yield big benefits for fisheries and conservation. *Fish. Fish.* 18, 128–144.
- Ewe, S.M., Gaiser, E.E., Childers, D.L., Iwaniec, D., Rivera-Monroy, V.H., Twilley, R.R., 2006. Spatial and temporal patterns of aboveground net primary productivity (ANPP) along two freshwater-estuarine transects in the Florida coastal everglades. *Hydrobiologia* 569, 459–474.
- Hammitt, K., 1990. Florida Land Use, Water Use, Streamflow Characteristics, and Water-Quality Characteristics of the Charlotte Harbor Inflow Area 1990. Land Use, Water Use, Streamflow Characteristics, and Water-Quality Characteristics of the Charlotte Harbor Inflow Area.
- Hussey, N.E., Kessel, S.T., Aarestrup, K., Cooke, S.J., Cowley, P.D., Fisk, A.T., Harcourt, R.G., et al., 2015. Aquatic animal telemetry: a panoramic window into the underwater world. *Science* 348, 1255642.
- Jørgensen, C., Dunlop, E.S., Opdal, A.F., Fiksen, Ø., 2008. The evolution of spawning migrations: state dependence and fishing-induced changes. *Ecology* 89, 3436–3448.
- Lowerre-Barbieri, S., Villegas-Ríos, D., Walters, S., Bickford, J., Cooper, W., Muller, R., Trotter, A., 2014. Spawning site selection and contingent behavior in common snook, *centropomus undecimalis*. *PLoS One* 9, e101809.
- Moses, C.S., Anderson, W.T., Saunders, C., Sklar, F., 2013. Regional climate gradients in precipitation and temperature in response to climate teleconnections in the Greater everglades ecosystem of South Florida. *J. Paleolimnol.* 49 (1), 5–14.
- Muller, R.G., Trotter, A.A., Stevens, P.W., 2015. The 2015 stock assessment update of Common snook, *centropomus undecimalis*. *Fla. Fish. Wildl. Res. Inst. IHR* 2015-004.
- Nguyen, V.M., Brooks, J.L., Young, N., Lennox, R.J., Haddaway, N., Whoriskey, F.G., Harcourt, R., et al., 2017. To share or not to share in the emerging era of big data: perspectives from fish telemetry researchers on data sharing. *Can. J. Fish. Aquat. Sci.* 74, 1260–1274.
- Peters, D.P., Lugo, A.E., Chapin, F.S., Pickett, S.T., Duniway, M., Rocha, A.V., Swanson, F.J., Laney, C., Jones, J., 2011. Cross-system comparisons elucidate disturbance complexities and generalities. *Ecosphere* 2 (7), 1–26.
- Peterson, C.D., Parsons, K.T., Bethea, D.M., Driggers III, W.B., Latour, R.J., 2017. Community interactions and density dependence in the southeast United States coastal shark complex. *Mar. Ecol. Prog. Ser.* 579, 81–96.

- Price, R.M., Swart, P.K., Willoughby, H.E., 2008. Seasonal and spatial variation in the stable isotopic composition ( $\delta^{18}\text{O}$  and  $\delta\text{D}$ ) of precipitation in south Florida. *J. Hydrol.* 358, 193–205.
- Rosenblatt, A.E., Heithaus, M.R., 2011. Does variation in movement tactics and trophic interactions among American alligators create habitat linkages? *J. Anim. Ecol.* 80, 786–798.
- Skjærraasen, J.E., Nash, R.D., Korsbrekke, K., Fonn, M., Nilsen, T., Kennedy, J., Nedreaas, K.H., et al., 2012. Frequent skipped spawning in the world's largest cod population. *Proc. Natl. Acad. Sci.* 109, 8995–8999.
- Stevens, P., Blewett, D., Boucek, R.E., Rehage, J.S., Winner, B., Young, J., Whittington, J., et al., 2016. Resilience of a tropical sport fish population to a severe cold event varies across five estuaries in southern Florida. *Ecosphere* 7, e01400.
- Stevens, P., Boucek, R.E., Trotter, A. A., Ritch, J. L., Johnson, E.R., Shea, C., Blewett, D.A., Rehage, J.S., (this issue) Illustrating the value of cross-site comparisons: habitat use by a large, euryhaline fish differs along a latitudinal gradient. *Fisheries Research*.
- Taylor, R., Grier, H., Whittington, J., 1998. Spawning rhythms of common snook in Florida. *J. Fish Biol.* 53, 502–520.
- Trexler, J.C., Loftus, W.F., Perry, S., 2005. Disturbance frequency and community structure in a twenty-five year intervention study. *Oecologia* 145 (1), 140–152.
- Trotter, A.A., Blewett, D.A., Taylor, R.G., Stevens, P.W., 2012. Migrations of common snook from a tidal river with implications for skipped spawning. *Trans. Am. Fish. Soc.* 141, 1016–1025.
- Underwood, A.J., 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. *Ecol. Appl.* 4 (1), 3–15.
- Young, J.M., Yeiser, B.G., Whittington, J.A., 2014. Spatiotemporal dynamics of spawning aggregations of common snook on the east coast of Florida. *Mar. Ecol. Prog. Ser.* 505, 227–240.
- Young, J.M., Yeiser, B.G., Ault, E.R., Whittington, J.A., Dutka-Gianelli, J., 2016. Spawning site fidelity, catchment, and dispersal of common snook along the East Coast of Florida. *Trans. Am. Fish. Soc.* 145 (2), 400–415.